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Foraging rhythm of great crested grebes *Podiceps cristatus* adjusted to diel variations in the vertical distribution of their prey *Osmerus eperlanus* in a shallow eutrophic lake in The Netherlands

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Summary. Great crested grebes *Podiceps cristatus* only foraged for an hour or two during dawn and again during dusk on Lake IJsselmeer in August-September. During this time of the year the adult birds are in wing moult and temporarily unable to fly. The food of grebes consisted almost exclusively of smelt *Osmerus eperlanus*, the most numerous pelagic fish. Simultaneous sonar registrations and trawl net fishing showed that smelt moved to the water surface during the twilight periods. During day and night they were concentrated near the bottom. We argue that grebes have the best foraging opportunities during twilight when much of their prey is near the surface, where light intensities allow the fish to be detected and captured. When the smelt are in the upper water layers the distance to be covered to get the prey (i.e. diving time and cost) is also least.

Key words: Diel rhythms – Vertical distribution of pelagic fish – Prey availability – Foraging – Fish-eating birds

Successful predators must properly respond to daily variations in the availability of their prey (Daan 1981). Studies in aquatic environments have yielded many examples of distinctive 24 h rhythms in foraging behaviour and distribution (*zooplankton*: Enright and Hamner 1967; Hutchinson 1967; Zaret 1980; Vuorinen 1987; *fish*: Thorpe 1978; *krill and fur seals*: Croxall et al. 1985). Seasonal and diel changes in the distribution of fish have been functionally explained as behavioural responses to optimize food intake (Narver 1970; Northcote and Rundberg 1970; Bohl 1980) and/or to reduce the risk of being preyed upon by predatory fish or fish-eating birds (Bohl 1980). We know only one study that has shown how fish-eating birds respond to daily variations in the behaviour of their prey (Sjöberg 1985).

This study aims to relate the diel feeding pattern of an avian fish predator, the great crested grebe *Podiceps cristatus*, to the vertical movements of its only prey at our study site, smelt *Osmerus eperlanus*.

Study area

The work was carried out in August-October 1985 and 1986 in Lake IJsselmeer, the largest lake in The Netherlands. Here large numbers of great crested grebes moult during August and September (Piersma et al. 1986). During this time the adults, which form the majority of grebes present, are temporarily flightless, and the grebe population is therefore relatively stationary (Piersma 1987).

Lake IJsselmeer consists since 1975 of two parts separated by a dike. Our study took place near the extensive shallows (1.5–3 m deep, see Fig. 1) along the eastern shore of the Northern part (52°50′N, 5°28′E). Lake IJsselmeer North has an average waterdepth of 4.5 m (maximum 17 m), with predominantly a sandy bottom. Following the early spring bloom of Bacillariophyceae, green and blue-green algae become dominant during summer and early autumn. Especially the eastern shallows become starting points for blooms of *Oscillatoria agardhii*, which in most years occur only locally. The deeper parts often have blooms of *Microcystis aeruginosa* (Berger 1987). Both the dense algal populations and the turbidity caused by wave action bringing bottom material in suspension, cause low transparency of the water column in August-October (Secchi disc values: 40–80 cm).

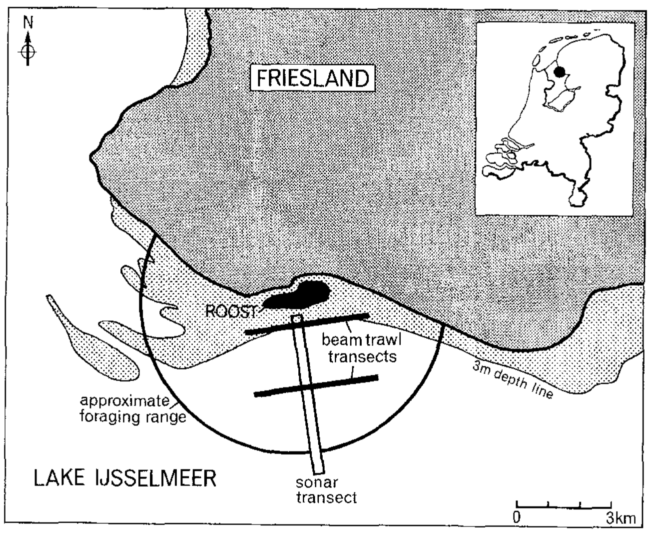

Fig. 1. Location of the study area (inset) and the transects relative to the roost of great crested grebes on the shallow water near the shore. The grebes foraged within a radius of approx. 5 km from the centre of the roost

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Methods

Great crested grebes were observed directly from the shore or from an elevated hide in the water near the shore, with a 15–60 X telescope. During the day, the activity of the grebes was regularly quantified by scan-sampling flocks as they were near the shore. The following behavioural categories were discerned: diving, flying, swimming/alert posture, preening and sleeping. Nocturnal observations were made with a light-intensifier (magnification 2.5–5 X). Further information on the daily movements and behaviour of grebes was collected 1) by recording the grebes' distribution and movements during (fishing) trips offshore (ca. 20 times in August-September 1985 and 1986) and 2) by recording movements of individual birds and small groups swimming on the flat water surface by ship-radar on the windstill night 17–18 September 1986.

It was impossible to quantify the foraging behaviour and food of grebes by direct observations on the open water. Instead, food composition was measured by analysing stomach contents of grebes that drowned in fishing nets in the study area in the period 1 August –15 October 1978–1986. No fish remains were found in the oesophagi of grebes collected during this time of the year. Details of processing stomach contents and estimating food composition are given by Piersma (1988).

The fish population was sampled with a 15 m long beam-trawl originally devised for catching eel *Anguilla anguilla*. The trawl had a mesh decreasing from 45 mm stretched width at the opening of the net to 15 mm at its end, with a bag of 10 mm mesh width. The opening was 7 m wide and 1.2 m high. When iron chain-weights of 60 kg were added to front of the trawl, the net was towed along the bottom. When the iron chains were removed, the trawl sampled the upper water layer, just under the water surface. Towing speed was held constant at 5 km/h. We covered two 4 km long transects at distances of 2 and 4 km from, and parallel to, the shore in the area where the great crested grebes fed (Fig. 1). Each traject was fished both along the surface and along the bottom, taking care not to cover the same path in successive tows. Fishing took place between 9 and 15 h. The fish was sorted in species and size classes. The fresh mass of these categories was taken with an accuracy of 5 g, and the numbers of individual fishes in these samples counted.

To monitor daily changes in fish distribution we used portable sonar equipment (Lowrance X-15 MA, pulse frequency 192 kHz, pulse length 1.3 millisec), installed alongside the vessel. On 17–18 September 1986 we traversed a 5 km long transect perpendicular to the shore into the lake (Fig. 1) eight times in the course of a 24 h period. Travel speed was 6–7 km/h. Continuous registrations were made on dry chart paper. Trials showed that there was a good correspondence between the density of sonar echo's and the size of the catch of pelagic fish, especially smelt (cf. Forbes and Nakken 1972; Argyle 1982). Good registrations of fish echo's started at a depth of 4 feet (1.2 m, see Fig. 4). We measured the density of echo's on eight 5 cm wide columns on the chart paper. These columns correspond to eight 100 m long segments of the standard transect, spread out evenly along the transect. Echo density was measured by counting the number of 1 mm^2 squares of transparent mm-paper overlay that contained any black of registered echo's. This number per water layer of 2 feet was taken as an index of the density of pelagic fish. Since the sonar sent pulses in a cone with an angle of 20°, the echo-density in successive depth layers was corrected for the increasing surface covered by the cone (4–6 feet: $\times 2.5$; 6–8 feet: $\times 1.8$; 8–10 feet: $\times 1.41$; 10–12 feet: $\times 1.18$; 12–14 feet: $\times 1$). To estimate the relative densities of smelt at different depth layers, a further correction was made by also multiplying the echo-density figure with the relative contribution of smelt to the total fish numbers, interpolating the values found by trawling along surface and bottom during daytime (see below, Table 2). Simultaneous to the sonar recording, a small trawl (1.8 by 4.5 m) with a mesh of 20 mm was towed along the surface. Catches made with this net yielded an impression of the kinds and relative densities of fish near the surface, in the course of the day. All times are in MET.

Results

On all the observation days, great crested grebes arrived on the shallow water near the shore in the course of the morning (Fig. 2A). On this area the grebes spent most of the time preening and sleeping (Fig. 2B). In the late afternoon the grebes left the area in southern directions, for the open water. Periods of arrival and departure are also indicated by the high proportions of grebes recorded in a swimming/alert posture (Fig. 2B). Almost no diving was seen near the shore (0.3% of a total of 43000 individual records): we conclude that no feeding took place on what we may call the roosting area. Observations with a light-intensifier (on 17–18 September 1986, Fig. 3 top, but also on 23–24 August 1986), and with the ship-radar (17–18 September 1986, Fig. 3 bottom) indicated that during the night the grebes returned from the open water to the roosting area to stay there for 5–6 h. Grebes were only observed foraging on the open water 2–6 km from the shore for 2–3 h in the early morning and for 2–4 h in the late afternoon and early evening. All foraging therefore took place around dawn and around dusk.

In the study area in August-October, great crested grebes ate almost exclusively smelt (Table 1). Some roach *Rutilus rutilus* and perch *Perca fluviatilis* were also eaten.

Two species dominated the fish community in the study area (Table 2). Smelt was the most numerous species, accounting for an overall 56% of the numbers caught (summing surface and bottom catches). Smelt contributed over 90% to the fish caught along the surface. Large (20–60 cm long) bream *Abramis brama* contributed most to the biomass (67%), but only occurred along the bottom.

By interpolating the relative contribution of smelt to total fish numbers as found on mid-day (Table 2), we have calculated the relative depth distribution of smelt from the sonar registrations at different times of the day (for an

Table 1. Diet composition of 25 juvenile and adult great crested grebes collected in the study area in Lake IJsselmeer between 1 August and 15 October 1978–1985

Species	Fish mass (g)	Percentage of fresh mass
Osmerus eperlanus	320	96.4%
Rutilus rutilus	8	2.4%
Perca fluviatilis	4	1.2%
Total	332	100%

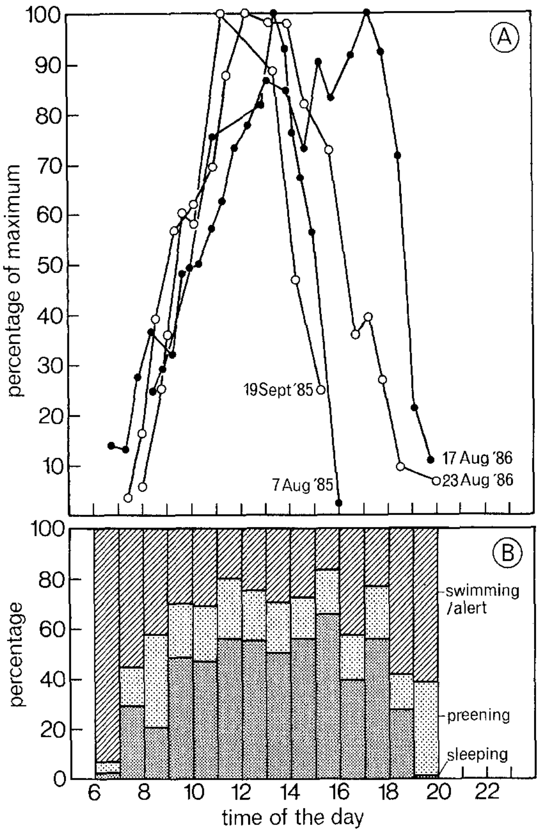

Fig. 2A, B. Daily changes in the relative number of great crested grebes on the roost on different dates in August-September 1985 and 1986 (**A**) and in their activity on the roost (**B**). Panel **B** shows observations made from the shore during 12 observation days in August-September 1986 (each hourly period at least 100 grebes were examined, total is 43000 individuals observed). Maxima are between 6000 and 15000 birds

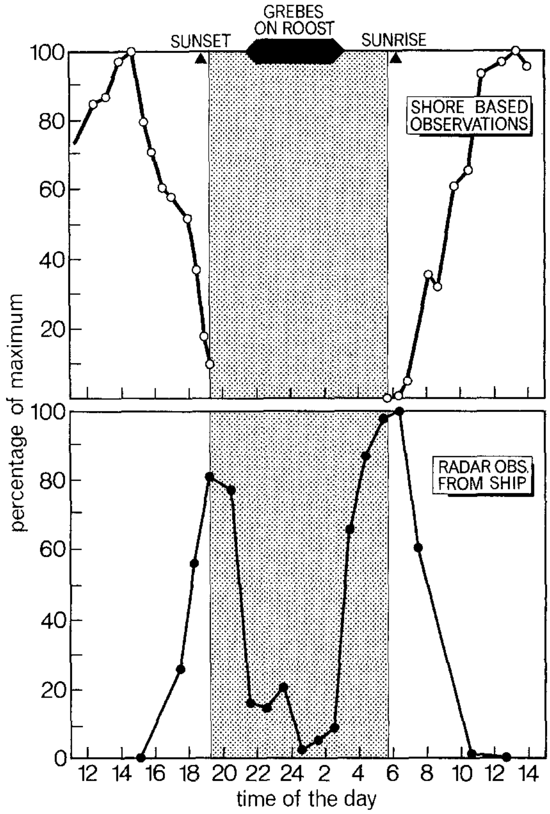

Fig. 3. Diel patterns in the distribution of great crested grebes in the study area. The top panel reports the observations made on 17–18 September 1986 both from the shore (*circles* indicate the relative numbers on the roost, maximum is 14000) and the bottom panel those made from the ship (the dots indicate the percentage of birds on water deeper than 3 m, as displayed on the ship's radar). The black bar indicates the period during the night when, from the shore with the light-intensifier, grebes could be seen on the roost, but numbers could not be quantified

Table 2. Composition by number (n) and by mass (m) of the catches of fish made with the beam trawl over 4 km long transects in the feeding area of great crested grebes. All yearclasses were taken together. Averages with SD's are presented for the catches made between 8 August and 15 October 1986

Species	Surface trawls ($n=6$)		Bottom trawls ($n=10$)	
	%n	%m	%n	%m
Anguilla anguilla	0	0	0.1 ± 0.1	0.2 ± 0.3
Osmerus eperlanus	90.7 ± 7.1	57.2 ± 32.8	47.4 ± 23.2	4.0 ± 5.6
Abramis brama	0.2 ± 0.6	14.1 ± 35.8	7.5 ± 7.5	68.0 ± 24.4
Rutilus rutilus	0.5 ± 0.8	12.5 ± 19.5	8.1 ± 10.3	7.9 ± 6.0
Gasterosteus aculeatus	0.8 ± 2.0	0.5 ± 1.5	0	0
Gymnocephalus cernua	0.9 ± 0.8	3.7 ± 4.9	13.3 ± 13.3	4.2 ± 5.8
Perca fluviatilis	6.8 ± 6.5	11.2 ± 5.6	21.7 ± 10.6	14.0 ± 11.2
Stizostedion lucioperca	0.1 ± 0.2	0.8 ± 2.0	1.8 ± 2.2	1.5 ± 2.0
Platichthys flesus	0	0	0.1 ± 0.1	0.2 ± 0.2
Total number	967 ± 970		3920 ± 2575	
Total mass (kg)		5.9 ± 11.5		233.3 ± 162.3

example see Fig. 4). Figure 5 shows that the smelt populations has a very distinct diel pattern of vertical movements. During the day and, to a lesser extent, during the night, most fish were found in the bottom layers. About 1–2 h around both dusk and dawn the fish distributed themselves over the entire water column, with most smelt present in the middle and top layers. Catches made along the water surface confirmed the pattern: the largest numbers of smelt were caught during the darker parts of the twilight period (Fig. 5 inset).

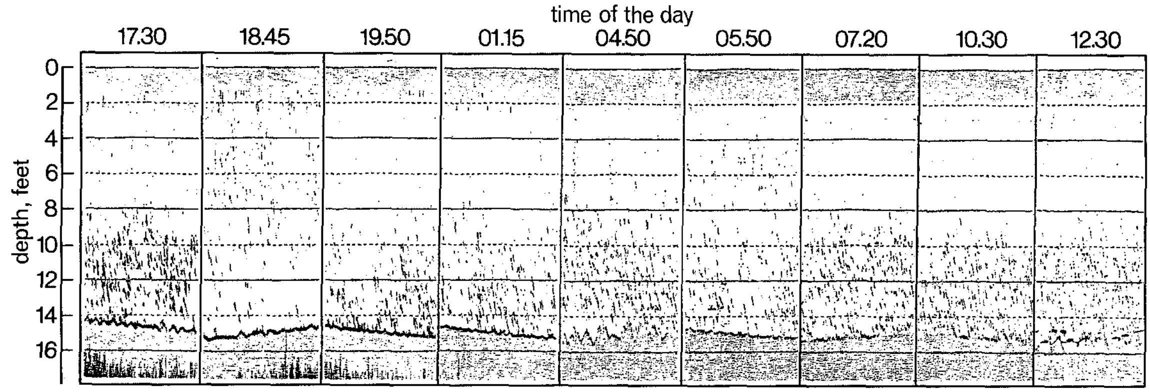

Fig. 4. Example of the sonar registrations of changes in vertical fish distribution. Examples of the registrations made on a "fixed" part of the transect on 17–18 September 1986 are presented. Note that the vessel covered the transect in alternating directions

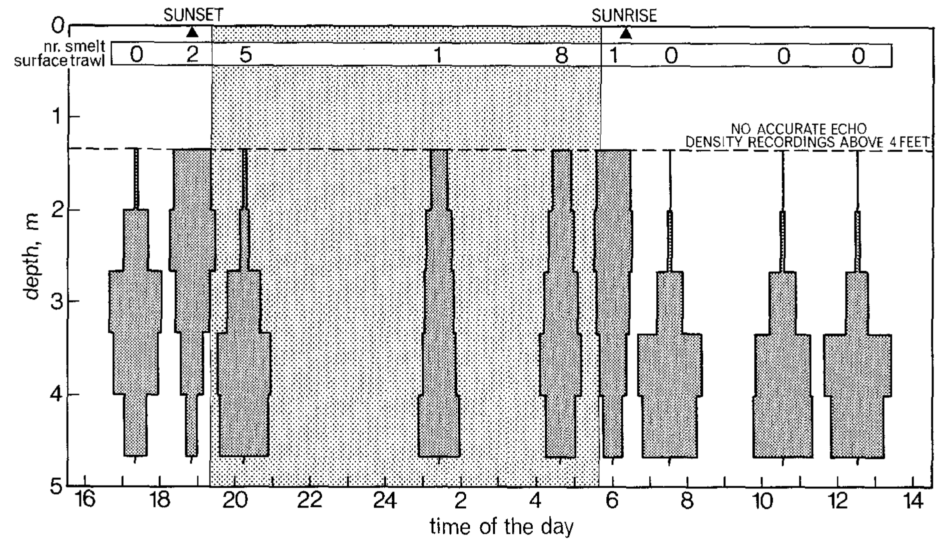

Fig. 5. Relative depth distribution of smelt in the course of a 24 h period on 17–18 September 1986, based on "corrected" densities of sonar-echo's. The relative abundance of smelt near the surface is given by the figures in the inset (data collected by towing a small net along the surface when covering the sonar-transect). See Methods for details

Discussion

Our findings are summarized in Fig. 6, showing the up- and downward movements of smelt around dawn and dusk, and simultaneously the occurrence of feeding by the great crested grebes. Although the visual capacity of pursuit-diving waterbirds like grebes has apparently never been studied (Lythgoe 1979), we must assume that they require at least 1% or 0.1% of the light intensity on the surface to be able to locate the prey (cf. Blaxter 1966). Figure 6 convincingly demonstrates that only after dawn and before dusk large numbers of smelt come into the zone where visual location by grebes would be possible. It is likely that smelt only show sufficient contrast to be spotted by the grebes, when they are approached from below (Hobson 1966; Lythgoe 1979). This means that the grebes have to dive deeper than where they catch the prey. Since diving is likely to entail a substantial energy cost, it always pays a grebe to forage when their prey is nearest to the surface. With reduced diving depths and diving times foraging is more energeticaly profitable (cf. Croxall et al. 1985).

Earlier studies have reported that great crested grebes often, but not always, feed in the twilight periods (Harrisson and Hollom 1932; Hanzák 1952; Simmons 1955, 1977; Mayr 1986). Crepuscular foraging was also noted in the piscivorous western grebe *Aechmophorus occidentalis* (Lawrence 1950). No author has yet related the timing of foraging by grebes to changes in the (vertical) distribution and the behaviour of the prey, although several independent studies have indicated that many pelagic fish species living in temperate lakes, which are of potential importance as food for grebes, often show distinct diel migration cycles (Narver 1970; Northcote and Rundberg 1970; Bohl 1980; Hamrin 1985). The lakes in which diel fish migration was found to occur, were all much deeper, and had a much higher transparency, than Lake IJsselmeer where Secchi-disc transparency was on average only 62 cm (SD = 18 cm, $n = 14$ days). Indeed, it is perhaps surprising that vertical migration of pelagic fish occurred at all in this type of lake. As asserted by Zaret (1980: p. 2), the vertical migration of zooplankton (a possible trigger for fish migration) is thought to be generally unimportant in shallow and turbid lakes. Bohl (1980) found that planktivorous fish in West German lakes showed no diel migration in winter (when they stayed near the bottom), while Simmons (1955) and Mayr (1986) report that, also in winter, the crepuscular foraging activity of non-breeding great crested grebes in England and West Germany is least pronounced. These observations fit very well into the pattern (a correlation between the occurrence of fish near the surface and the timing of feeding by grebes) described in this study.

Two factors directly related to fish behaviour, may addi-

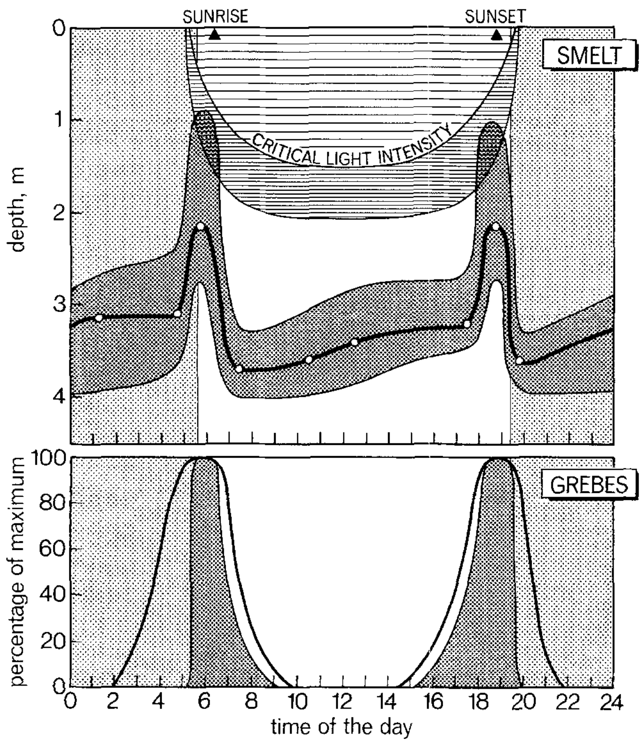

Fig. 6. Summary of the diel changes in the vertical distribution of smelt and the depths of which critical light intensities reach (*top*) and in the feeding activity of great crested grebes (*bottom*). Changes in the depth distribution of smelt were calculated from the data in Fig. 5, extrapolating echo densities to surface level. Averages ±25% intervals are given by the heavily shaded area (i.e. 50% is shaded). The critical light intensity range is bordered by the calculated depths down to which 1% (upper line) and 0.1% (lower line) of the surface light intensity at midday occur, in lake-water with a measured transparency of 60 cm Secchi-disc value (C. in litt. Berger). The feeding activity of grebes is given by the percentage of birds on the offshore feeding area (heavy line, from Fig. 3) and the proportion actually diving (shaded area, from occasional observations from vessels)

tionally facilitate the foraging of grebes during twilight. Pelagic fish which come to the surface during dusk, sometimes the night, and during dawn, have been shown to also feed (on zooplankton) during these periods (Narver 1970; Bohl 1980). Since foraging activity may interfere with the fishes' capacity of detecting predators (Metcalfe et al. 1987), foraging fish may be relatively easy to capture. The second factor relates to a possible effect of schooling. Detailed studies have shown that schooling by small fish may reduce the effectiveness of, or even preclude, the predator's attack, especially in dark and turbid water (Hobson 1968; Neill and Cullen 1974). Figure 4 shows that echo's reach highest densities when the fish are near the bottom. This suggests that smelt may live in schools during the day and during the night. When they start foraging in the twilight periods, schools break up and smelt move about independently, possibly to enable their own (visual) feeding on zooplankton. When outside the school and while feeding, smelt will be most easily captured by the hunting grebes.

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